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3 Expected genetic response for oleic acid content in pork[1]

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ABSTRACT: Intramuscular fat (IMF) and oleic acid (C18:1) content in pork are two important issues for the pig industry and consumers. Data from a purebred Duroc line were used (1) to estimate the genetic parameters of IMF and C18:1 and their genetic correlations with lean growth components and (2) to evaluate the opportunities for genetically improving C18:1 in IMF. The data set used for the estimation of the genetic parameters consisted of 93,920 pigs, from which 85,194 had at least one record for BW or backfat thickness (BT) at 180 d and 943 for IMF and C18:1 at 205 d. Intramuscular fat content and C18:1, expressed as percent of total fatty acids, were determined in the gluteus medius muscle by gas chromatography. Genetic parameters for C18:1 were estimated under a Bayesian 4-trait multivariate animal mixed model. Heritability of C18:1 was 0.50, with a probability of 95% of being greater than 0.37. The genetic correlations of C18:1 with BW, BT, and IMF were 0.11, 0.22, and 0.47, respectively (with a probability of 95% of being greater than -0.07, 0.04, and 0.27, respectively). Genetic responses were evaluated by deterministic simulation using a half-sib recording scheme for C18:1 and the previously estimated parameters. The C18:1 content is expected to exhibit only minor changes in selection programs directed at growth rate but to decrease in those focusing on lean content. Maximum expected response in C18:1 at no lean growth loss (i.e., at no change in BW and BT) was 0.44%, with a resulting correlated response in IMF of 0.15%. However, as lean growth is emphasized in the breeding goal, the resulting response scenarios are more constrained. It is concluded that there is strong evidence supporting that C18:1 in IMF is genetically determined and that there exist selection strategies leading to response scenarios in which C18:1, IMF, BT, and BW can be simultaneously improved. However, if adopted, the potential for lean growth would be reduced. The extent to which it is affordable relies on how much consumers are prepared to pay for high-C18:1 pork products.

Key words: genetic parameters, intramuscular fat, meat quality, oleic, pigs, selection

INTRODUCTION

Fat content and composition are two important issues for the pig industry and consumers. Intramuscular fat (**IMF**) and oleic acid (**C18:1**) contents are two of the traits that have attracted greatest interest over the last years. The IMF content has been favorably related to the tenderness and juiciness of cooked meat (Wood et al., 2008), as well as to technological and sensorial properties of dry-cured products (Ruiz-Carrascal et al., 2000). The C18:1 content has been traditionally considered a key quality criterion in dry-cured products because of its positive role in the manufacturing process and in flavor (Toldrá, 2002). More recently, owing to its associated benefits for human health (Christophersen and Haug, 2011; Jiménez-Colmenero et al., 2010), C18:1 is also becoming an appreciated trait in some niche markets of fresh meat.

Both IMF and C18:1 are affected by dietary and genetic factors (De Smet et al., 2004). It is known that IMF, despite being unfavorably correlated with carcass lean content, can be efficiently selected (Suzuki et al., 2005). However, there is still little evidence on the opportunities for genetic change in fatty acid (**FA**) composition. Recent studies in this regard, although promising, were either based on small and heterogeneous data sets (Ntawubizi et al., 2010; Sellier et al., 2010) or, regarding C18:1, not conclusive enough (Casellas et al., 2010). Moreover, because the challenge for the industry is to develop selection criteria not only aimed at increasing C18:1 but at the whole profit of a line, the genetic correlation structure of C18:1 with other economic traits, particularly with lean growth, is needed. Therefore, the aims of this study were (1) to estimate the heritability of C18:1 and its genetic correlations with IMF and lean growth in pigs from a Duroc line primarily used for producing high quality dry-cured

hams and (2) to discuss the opportunities for genetically improving C18:1 under different selection scenarios.

MATERIAL AND METHODS

All experimental procedures were approved by the Ethics Committee for Animal Experimentation of the University of Lleida.

Animals and Sample Collection

Data from a purebred Duroc line were used for the analyses. The line was completely closed in 1991 and since then it has been selected for an index including BW, backfat thickness (**BT**), and IMF (Solanes et al., 2009). The data set used for the estimation of the genetic parameters consisted of 93,920 pigs, from which 85,253 had at least one recorded trait. Pigs with records were born from 1996 to 2009. At about 75 d of age piglets were moved to the fattening units, where they were penned by sex (8 to 12 pigs per pen) until slaughter. All pigs were performance-tested at an average age of 180 d for BW and BT. Backfat thickness was ultrasonically measured at 5 cm off the midline at the position of the last rib (Piglog 105, Herlev, Denmark). During the test period pigs had ad libitum access to commercial diets. Since 2002 a sample of the purebred barrows used for producing dry-cured ham was taken for recording IMF and C18:1. Two barrows per litter were taken from fixed litters chosen either at random or selected according to the mid-parent BLUP breeding values for BW and BT at 180 d. These barrows were raised in 12 batches until slaughter at around 205 d. From 160 d onwards barrows were fed a commercial pelleted finishing diet (Esporc, Riudarenes,

99Girona, Spain) with an average composition of 16.9% crude protein, 6.59% fiber, and
1006.66% fat (C16:0: 20.8%; C18:0: 7.1%; C18:1: 35.4%; C18:2: 27.4%). Feed in each
101batch was analysed in triplicate as described in Cánovas et al. (2009). At the end of the
102finishing period the barrows were slaughtered in a commercial slaughterhouse. After
103chilling for about 24 h at 2ºC, a sample of at least 50 g of the gluteus medius muscle
104was taken from the left side ham, immediately vacuum packaged, and stored in deep
105freeze until required for IMF and C18:1 determination. A summary of the population
106characteristics and number of records, sires, dams, and litters used for each analyzed
107trait is given in Table 1.
108
109***Fat Analysis***
110 After gluteus medius samples were completely defrosted and vacuum drip losses
111were eliminated, the dissected muscle, trimmed of subcutaneous and intermuscular fat,
112was minced. A representative aliquot from the pulverized freeze-dried muscle was used
113for fat analysis. Intramuscular fat content and composition was determined in duplicate
114by quantitative determination of the individual FA by gas chromatography (Bosch et al.,
1152009). Fatty acid methyl esters were directly obtained by transesterification using a
116solution of 20% boron trifluoride in methanol (Rule, 1997). Methyl esters were
117determined by gas chromatography using a capillary column SP2330 (30 m × 0.25 mm,
118Supelco, Bellefonte, PA) and a flame ionization detector with helium as carrier gas.
119Runs were made with a constant column-head pressure of 172 kPa. The oven
120temperature program increased from 150 to 225ºC at 7ºC per min and injector and
121detector temperatures were both 250ºC. The quantification was carried out through area
122normalization after adding into each sample 1,2,3-tripentadecanoylglycerol as internal
123standard. Intramuscular fat content was calculated as the sum of each individual FA

expressed as triglyceride equivalents (AOAC, 1995). Oleic acid content was calculated as the percentage of C18:1 relative to total FA in IMF. Fatty acids were identified by comparing their relative retention times with those of the external standard and confirmed by comparing their mass spectra to the computer library of the GC/MS database Wiley 275.L and NBS 75 K.L. Fatty acids were analyzed on a simple quadrupole instrument (GC/MSD 6890N-5973N, Agilent Technologies, Wilmington, DE) equipped with an electron ionization source using the same temperature program as described above. Scanned mass range of FA was m/z 35-450 and the scanning rate 3.46 scans/s.

Estimation of Genetic Parameters

Genetic parameters for BW, BT, IMF, and C18:1 were estimated fitting a 4-trait multivariate animal model. In matrix notation, the model was:

$$\mathbf{y}_i = \mathbf{X}_i \mathbf{b}_i + \mathbf{Z}_i \mathbf{a}_i + \mathbf{W}_i \mathbf{c}_i + \mathbf{e}_i ,$$

where $\mathbf{y}_i$ is the vector of observations for trait i (BW, BT, IMF, and C18:1); $\mathbf{b}_i$, $\mathbf{a}_i$, $\mathbf{c}_i$, and $\mathbf{e}_i$ are the vectors of systematic, additive genetic, litter, and residual effects, respectively; and $\mathbf{X}_i$, $\mathbf{Z}_i$, and $\mathbf{W}_i$, the known incidence matrices that relate $\mathbf{b}_i$, $\mathbf{a}_i$, and $\mathbf{c}_i$ with $\mathbf{y}_i$, respectively. Systematic effects for BW and BT were the batch (1039 levels), gender (3 levels; males, females, and castrates), and age at measurement as a covariate. Pigs tested at the same time and in the same unit were considered as one batch. The same model was used for IMF and C18:1 but with systematic effects only including the batch (12 levels) and the age at measurement (or carcass weight). Because there were only 1.7 piglets per litter with records on IMF and C18:1, the litter was dropped from the model

149for these two traits. Intramuscular fat content and C18:1 were analyzed using either the 150raw data or the following u_1 and u_2 isometric log-ratio (ilr) transformed variables 151(Egozcue *et al*., 2003):

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153 $$u_1 = \frac{1}{\sqrt{6}} \ln\left(\frac{C18:1 \times (100 - C18:1) \times (IMF/100)^2}{(100 - IMF)^2} \right)$$

154and

155 $$u_2 = \frac{1}{\sqrt{2}} \ln\left(\frac{C18:1}{(100 - C18:1)} \right),$$

156

157where (100-IMF) + [C18:1 + (100-C18:1)] × IMF/100 = 100.

158 Genetic parameters were estimated in a Bayesian framework using Gibbs 159sampling with the TM software (Legarra et al., 2008). The traits were assumed to be 160conditionally normally distributed as follows:

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162 $$\begin{bmatrix} y_1 \\ y_2 \\ y_3 \\ y_4 \end{bmatrix} \Big| \, \mathbf{b}_1, \mathbf{b}_2, \mathbf{b}_3, \mathbf{b}_4, \mathbf{a}_1, \mathbf{a}_2, \mathbf{a}_3, \mathbf{a}_4, \mathbf{c}_1, \mathbf{c}_2, \mathbf{R} \sim \mathrm{N}\left(X \begin{bmatrix} b_1 \\ b_2 \\ b_3 \\ b_4 \end{bmatrix} + Z \begin{bmatrix} a_1 \\ a_2 \\ a_3 \\ a_4 \end{bmatrix} + W \begin{bmatrix} c_1 \\ c_2 \end{bmatrix}, R \right),$$

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164where **R** was the (co)variance matrix. Sorting records by pig, and trait within pig, **R** 165could be written as $\mathbf{R}_0 \otimes \mathbf{I}$, with $\mathbf{R}_0$ being the 4 × 4 residual (co)variance matrix between 166the four traits analyzed and **I** an identity matrix of appropriate order. Flat priors were 167used for $\mathbf{b}_i$ and residual (co)variance components. Additive genetic and litter values, 168conditionally on the associated (co)variance components, were both assumed 169multivariate normally distributed with mean zero and with (co)variance $\mathbf{G} \otimes \mathbf{A}$ and $\mathbf{C} \otimes$

I, respectively, where **A** was the numerator relationship matrix, **G** was the 4 × 4 genetic relationship matrix between the four traits, and **C** was the 2 × 2 (co)variance matrix between litter effects of BW and BT. The matrix **A** was calculated using all the pedigree information summarized in Table 1. Flat priors were used for additive and litter (co)variance components. Statistical inferences were derived from the samples of the marginal posterior distribution using a unique chain of 2,000,000 iterations, where the first 250,000 were discarded and one sample out of 100 iterations retained. Statistics of marginal posterior distributions and the convergence diagnostics were obtained using the BOA package (Smith, 2005). Convergence was tested using the *Z*-criterion of Geweke and visual inspection of convergence plots.

Prediction of Expected Responses

The expected genetic response for C18:1 from a simulated breeding program was compared in two recording scenarios. In the first, it was assumed that records on C18:1 were not available and selection was only directed at either increasing BW (or IMF) or decreasing BT, while, in the second, records on C18:1 were available and C18:1 was proactively selected. The selection objective in each case was derived as the linear combination of the appropriate breeding values weighted by their economic values. Economic weights were determined iteratively using a desired-gains approach until the desired combination of genetic gains was achieved. For simplicity, only some illustrative cases in each scenario are presented. A population with discrete generations was simulated in which 40 boars were randomly mated to 400 sows with a mating ratio of 1 boar to 10 sows. The breeding scheme consisted of two selection stages resulting in the top 25% males and 50% females, with the same selection pressure in each stage. Two males and two females from the offspring of each sow were performance-tested at

180 d for BW and BT. In the second stage, three of the culled individuals per sire family were slaughtered to determine IMF, in the first scenario, and also C18:1, in the second. Pigs in the first stage were selected on the individual, full-sib and half-sib phenotypic performance of BW and BT, and the pedigree information (BLUP) of all recorded traits. Selection on the second stage was additionally based on the new half-sib records on IMF and, if available, C18:1. Only the first stage but with the whole selection pressure was applied in cases where neither IMF nor C18:1 were recorded. Selection response was predicted by deterministic simulation of a two-stage selection scheme with discrete generations using the program SelAction (Rutten et al., 2002). The program accounts for reduction in variance due to selection (Bulmer, 1971) and corrects selection intensities for finite population size and for the correlation between index values of family members (Meuwissen, 1991).

RESULTS

Phenotypic Values and Environmental Effects

The average phenotypic value of C18:1 in IMF was 44.8%, with an IMF content of 4.9% (Table 1). The effects of batch and age at slaughter on C18:1 are given in Table 2. On average, the variation among batches accounted for 2.4% of C18:1, with a maximum difference between batches of 7.5%. The effect of age at slaughter on C18:1 was low but negative (-0.02%/d). There was not much evidence for the environmental effect of the IMF content on C18:1, with a mean value of zero but showing a large highest density interval at 95%, ranging from -0.31% to 0.26% per unit of percentage of

IMF. The environmental effect of the carcass weight was positive, with a mean value of 0.02%/kg, with a probability of 95% of being greater than zero.

Genetic Parameters

Estimates of the variance components and heritabilities for BW, BT, IMF, and C18:1, together with the respective genetic and residual correlations among each other, can be seen in Table 3. Specific features concerning the posterior distribution of the heritability of C18:1 and the genetic and phenotypic correlations of C18:1 with BW, BT, and IMF are given in Table 4. The correlation between litter effects in BW and BT was 0.58 (SD 0.02). The value of the heritability for C18:1 was high (0.50, SD 0.08) and very similar to that for IMF (0.56, SD 0.09), with a probability of 95% of being higher than 0.37. The genetic and phenotypic correlations of C18:1 with IMF were moderate and positive, with a 95% probability of being higher than 0.27 and 0.29, respectively. The genetic and phenotypic correlations with BW and BT were also all positive, although lower, with values in the range of 0.11 to 0.22. Results did not provide conclusive evidence concerning the sign of the genetic correlation between C18:1 and BW, where the associated highest posterior density interval at 95% ranged from -0.10 to 0.31. No substantial deviations in the estimates were observed after adjusting C18:1 for carcass weight or IMF content, or, on the other hand, when the ilr-transformed variables u_1 and u_2 were used in the analyses instead of IMF and C18:1 (Table 5). As compared to the reference case, where C18:1 was only adjusted for age at slaughter, the estimates of the heritability of C18:1 after alternatively adjusting C18:1 for carcass weight, age plus IMF content, or carcass weight plus IMF content were only slightly higher, with a maximum value of 0.55. Similar values were obtained for the differently adjusted genetic correlations of C18:1 with BW, BT, and IMF, except for the

correlation between C18:1 adjusted for carcass weight and BW, where, as expected, values decreased to almost zero. When the ilr-transformed variables were used, the maximum change occurred for the genetic correlation between C18:1 and BT, which decreased from 0.22 to 0.18. Because only minor changes were seen across models and data transformation, responses below were calculated using the estimates in Table 3.

Expected Responses

Indirect expected responses in C18:1 to selection for BW, BT, or IMF are given in Table 6. In the first scenario, where records on IMF are not available, at best no change in C18:1 is expected. In most sire lines the breeding goal is directed at increasing lean growth. According to the emphasis put in each of the two components of the trait, the selection objective in these lines can be placed in-between maximizing BW at restrained BT, in one extreme, and minimizing BT at restrained BW, in the other. Thus, within this scenario, the best situation occurs when selection is for BW at restrained BT, in which case only little changes in C18:1 are expected. However, as selection against BT is emphasized, C18:1 declines up to values around 0.2% per generation, when BW is constrained to remain unchanged. This decrease in C18:1 can be minimized if records on IMF are available. Thus, in this new scenario, if IMF is also restrained, the decrease in C18:1 is reduced 3-fold. Moreover, if IMF is proactively selected, there is room for favorable responses in C18:1. Increasing IMF at restrained BW and BT led to similar but opposite response in C18:1 than decreasing BT at restrained BW. Response in C18:1 can be further improved if it is directly selected (Figure 1). There exist selection scenarios leading to favorable responses in all traits, for instance, 1 kg in BW, -0.25 mm in BT, 0.06% in IMF, and 0.25% in C18:1. Maximum expected response in C18:1 at no lean growth loss (i.e., at no change in BW and BT) is 0.40%, with a resulting correlated

response in IMF of 0.15%. Increasing the emphasis in both BW and against BT constricts the response curves.

DISCUSSION

Results obtained provide strong evidence that C18:1 content in IMF is genetically determined. The estimate of the heritability of C18:1, with a value around 0.50, is in line with that obtained by Ntawubizi et al. (2010) with crossbred pigs but higher than other estimates, which were in the range of 0.26 (Sellier et al., 2010), in Landrace and Large White, to 0.36 (Suzuki et al., 2006), in Duroc. In the present study, as in Suzuki et al. (2006), inferences were based on a Duroc line with known selection trajectory, but using a bigger data set and a more representative family structure across generations. Similar values have been reported for the heritability of C18:1 in the backfat of Duroc pigs, with values ranging from 0.26 (Suzuki et al., 2006) to 0.57 (Gjerlaug-Enger et al., 2011). Estimates obtained in other breeds for the heritability of C18:1 in the subcutaneous fat showed a similar trend, with values from 0.30 in Iberian pigs (Fernández et al., 2003) to as high as 0.67 in Landrace (Gjerlaug-Enger et al., 2011).

The high value for the heritability of C18:1 is maintained even when adjusted for IMF, showing a negligible probability of being lower than 0.28 ($P < 0.001$). This finding removes the concerns raised by Casellas et al. (2010) about the genetic determinism of C18:1 at fixed IMF. However, this result contrasts with the dramatic reduction, from 0.58 to 0.18, observed by Ntawubizi et al. (2010) for the heritability of C18:1 after adjusting for IMF. These later authors suggested that this might be due to the low IMF content showed by their experimental crossbred pigs (1.2%), a situation where small variations in IMF, mostly dominated by changes in PUFA, may have a

great impact. Our results, which were obtained in a population displaying 4-fold higher IMF than theirs, would support this hypothesis. However, note that here, because estimates are based on a 4-trait analysis, with IMF being one of the traits, and not on a series of univariate analyses, the genetic effect is subtracted from IMF when acting as a covariate, then giving as a result a lower effect of IMF on C18:1. In fact, the effect of IMF on C18:1 was much greater in a 3-trait analysis excluding IMF (0.33, SD 0.04) than in the full 4-trait analysis (0.01, SD 0.14). The heritability of C18:1 in the 3-trait analysis was lower (0.45, SD 0.08) but still very conclusive with respect to the genetic determination of C18:1. Taken as a whole, the results indicate that C18:1 displays a moderate-to-high heritability and suggest that there is potential for improving C18:1 in IMF by selection.

Selection responses in C18:1 should be put into context with the correlated genetic change in other economic traits. In this study C18:1 showed a favorable and moderately high genetic correlation with IMF, in accordance with the observed trend of FA composition with IMF in this line (Bosch et al., 2012), but much higher than that reported by Suzuki et al. (2006), the only other study that examined the genetic relationship between C18:1 and IMF, which was 0.10. Although positive and low, there is less evidence on the magnitude of the genetic correlations of C18:1 with BW and BT, particularly for BW, where negative values cannot be discarded completely. Reported estimates for the correlation between C18:1 and BW are more consistent with the values encountered here than those for the correlation between C18:1 and BT (Suzuki et al., 2006; Ntawubizi et al., 2010). Suzuki et al. (2006) observed that C18:1 and BT are almost uncorrelated while Ntawubizi et al. (2010) found that they are positively correlated (0.40). Owing to the fact that the genetic correlation among C18:1 at different fat depots is high, around 0.7 (Suzuki et al., 2006), complementary information can be

retrieved from results on C18:1 at other fat tissues than IMF. Results for backfat C18:1 give a similar contradictory picture: while some authors (Cameron et al., 1990; Fernández et al., 2003) found that C18:1 and BT are hardly correlated (around 0.10), others reported that they are unfavorably related (Gjerlaug-Enger et al., 2011). Intramuscular fat content showed a similar genetic correlation structure with BW and BT than C18:1, in agreement with previous results in the same Duroc population (Solanes et al., 2009).

Discrepancies in the above estimates may arise because of differences in the age or weight at test and in the muscle where IMF and C18:1 are measured. In the present study, pigs were tested for BW and BT at 180 d while IMF and C18:1 were determined analytically in the gluteus medius muscle at 205 d. Results in Solanes et al. (2009) showed that the genetic correlation of IMF with BW and BT, both traits measured at 180 d, were higher than those found here for IMF at 205 d. This could indicate that the genetic relation between performance traits, particularly for BW and IMF-related traits, including C18:1, decreases as age increases. In fact, in heavy Iberian pigs, Fernández et al. (2007) even found that the correlation between BW and IMF was negative. This might be interpreted in light of the fact that C18:1 evolves linearly with age throughout the studied period whereas BW and BT do not (Bosch et al., 2012). The muscle and the determination method of IMF may also influence the relationship among fat depots. Here C18:1 was measured in the gluteus medius instead of LM, as in most reported estimates, because sampling from gluteus medius is easier and cheaper as compared to LM. Muscles behave differently in terms of both IMF content and composition and, because gluteus medius is fatter than LM at a given age (Casellas et al., 2010), IMF in gluteus medius may be more correlated to overall fatness (Solanes et al., 2009). Variations in age, slaughter weight, and IMF content are commonly adjusted including a

344covariate in the model describing the data. The magnitude of these covariates for C18:1
345in the 4-trait analysis was very low and therefore inferences concerning C18:1 did not
346relevantly change across models. Major differences occurred when adjusting for carcass
347weight, likely because in this case the covariate is capturing part of the deviations
348between BW at 180 d and carcass weight at 205 d. Similarly, no relevant changes in the
349estimates of the genetic parameters were observed after the isometric log-ratio
350transformation of IMF and C18:1. Note that both IMF and C18:1 are compositional data
351in nature (Aitchison, 1986), so conceptually they cannot be used in real space unless
352they are previously transformed (Egozcue et al., 2003). However, Estany et al. (2011),
353using real and simulated data, have already shown that, in regard to IMF and C18:1,
354transformed values only performed a little better when predicting future records of IMF.
355 Data on FA composition have often been obtained from experiments designed for
356other purposes or from culled pigs, and therefore they are not necessarily randomly
357chosen. In such cases, data may be subjected to selective recording and inferences on
358genetic parameters may be biased. However, if the history of the selection process is
359contained in the data employed in the analysis, then the posterior distribution has the
360same mathematical form with or without selection (Gianola and Fernando, 1986). In
361this study, the pigs in which IMF and C18:1 were determined were chosen exclusively
362on the BLUP of the breeding values of BW and BT from the pedigree and records used
363in the present analysis. All estimates shown here were derived under this principle and
364therefore they were implicitly adjusted for selective recording. Inferences obtained
365using only data from pigs with records on C18:1, although they did not affect the
366estimate of the heritability of C18:1, underestimated the genetic correlations of C18:1
367and IMF with BW and BT, even suggesting a negative genetic relationship of BW with
368IMF and C18:1 (results not shown). Including all the data in the analysis removed the

effect of selection and put in evidence the risks of estimating genetic parameters, particularly correlations, using data recorded for other purposes.

Expected responses suggest that breeding programs directed at increasing C18:1 are feasible but also that this genetic progress is achieved at the expense of decreasing lean content. In many instances the correlated change in C18:1 to selection for production traits is likely more important than the execution of direct selection. In this scenario, our results show that selection for lean growth will not lead to favorable changes in C18:1, which will only be indirectly improved in breeding regimens selecting proactively for IMF. Some experiments have already demonstrated that it is possible to increase IMF through selection (Suzuki et al., 2005; Schwab et al., 2009). The low expected responses in C18:1 and IMF to selection for BW at restrained BT indicate that, if selection gives a great emphasis on growth rate, little changes in both IMF and C18:1 should be expected. This result is consistent with experimental evidence indicating that continuous selection for lean growth did not necessarily lead to decreased IMF (Oksbjerg et al., 2000; Tribout et al., 2004).

Direct selection for C18:1 allows for convenient scenarios in which C18:1, IMF, BW, and BT can be simultaneously improved. A desired-gain approach was used to determine the weights for traits in the breeding objective. This is a useful approach for traits not yet included in the payment system or subjected to restrictions, as established in some labeled products. In fact, restricted values on FA are a common feature in regulations for foods bearing nutritional or health claims concerning fat properties and, in particular, a minimum C18:1 and a maximum C16:0, C18:0, and C18:2 contents are common requirements in grading Iberian cured products. However, proper economic weights are needed to achieve the optimum response profile in each situation. It has been proposed using interviews to experts or market surveys as input for developing a

394pricing system based on a quantitative differentiation of willingness-to-pay values for
395carcasses of different qualities (von Rohr et al., 1999). The method has been used in the
396Swiss breeding program for calculating the economic value of fat quality, indirectly
397measured as the amount of double bonds in FA in the outer layer of backfat (Hofer et
398al., 2006). To our knowledge this is so far the only published attempt to select for fat
399composition in pigs, although no realized responses have been reported yet. A similar
400approach can be used to elucidate the economic value of traits, such as C18:1, reflecting
401possible future trends of the pork market.

402 Selection for C18:1 leads to an undesired correlated response in BT (i.e., lean
403content) and to genetic lag in BW (i.e., average daily gain). Then, for a given scenario,
404the opportunity cost of selecting for increased C18:1 can be derived by subtracting the
405total economic response weight in the adopted scenario from the maximum total
406economic response. Alternatively, in case of being negative, this difference can also be
407interpreted as an estimation of the societal benefits of selecting for healthiness (Kanis et
408al., 2005). Other economic traits not included in the present analysis may also show
409undesired responses. There have not been reported estimates on the genetic correlation
410of C18:1 in IMF with feed conversion ratio, proportion of premium cuts, or prolificacy.
411However, results relating to C18:1 (Fernández et al., 2003) and C18:2 (Hofer et al.,
4122006) in backfat lead to expected unfavorable correlated responses in both feed
413conversion ratio and proportion of premium cuts, although not to premium pieces
414weight. On the other hand, in accordance with Solanes et al. (2009), who found that
415IMF was uncorrelated to prolificacy, no relevant genetic change in prolificacy is
416expected after selection for C18:1.

417 Genetic differences between individuals for C18:1 in IMF may come from
418differential ability of pigs either to incorporate dietary C18:1 to IMF or to synthesize

419C18:1 from C16:0 and C18:0 via increased enzymatic activity of elongases and delta-9
420desaturases, respectively. Cánovas et al. (2009) found that selection for decreased BT at
421restrained IMF led to decreased expression of both enzymes in backfat but not in IMF,
422giving support to the hypothesis that the metabolic pathways underlying the synthesis of
423C18:1 are altered by selection. From a practical view, however, the question whether
424selection for increased C18:1 content is affordable must be contrasted versus the cost-
425benefit ratio of alternative strategies. Diet and age at slaughter, which partly explain the
426variation among batches for C18:1, are the two most used practices to improve both
427IMF content and composition. However, experimental results indicate that the impact of
428dietary FA additions mainly affects subcutaneous fat and PUFA rather than IMF and
429MUFA (Wood et al., 2008). Despite it has been shown that feeding pigs with high-oleic
430diets may increase C18:1 in IMF by up to 3% (Mas et al., 2010), this approach has not
431always been successful (Mas et al., 2011). In general, major changes in C18:1 are
432achieved indirectly by raising IMF content. Teye et al. (2006), using a low protein diet,
433and Bosch et al (2012), delaying the age at slaughter, two management practices aimed
434at improving IMF, increased C18:1 by values in the range of 4-7%. However, results
435here indicate that, on average, batch differences only accounted for around 2% of
436C18:1, approximately the expected genetic change that would be achieved after 5
437generations of selection.

438 A limitation for implementing direct selection for C18:1 is that phenotypes
439cannot be observed on the selection candidates themselves and are costly to determine.
440It is difficult to measure C18:1 in live animals unless biopsies (Bosch et al., 2009) or
441genetic markers (Estellé et al., 2009) are used. However, the first approach is mostly
442restricted to experimental designs whereas the second has not yet been able to translate
443advances into effective commercial improvements (Dekkers, 2004). The use of

444increasingly accurate on-line equipments, such as those based on the near-infrared
445spectroscopy (Gjerlaug-Enger et al., 2011; Shackelford et al., 2011), represents an
446opportunity for systematic recording C18:1 on the slaughter chain. Due to higher
447measurement errors, lower heritability values may be expected using such records in
448relation to analytical methods (Fernández et al., 2003). However, the estimate of the
449heritability of IMF obtained here is in line with a previous one obtained in the same
450Duroc population but using data taken with a near infrared transmittance spectrometry
451device (Solanes et al., 2009). Accordingly, no relevant changes should be expected by
452using on-line measurement technologies. Other direct alternative methods specifically
453directed to determine C18:1 content have also been proposed (Muñoz et al., 2011).

454 Two questions were addressed in this study, first, whether there is genetic
455variation in C18:1 content in IMF and, second, which response scenarios are expected
456for indirect and direct selection. It is concluded that selection for C18:1 content in IMF
457can be effective and that there exist selection strategies leading to response scenarios in
458which C18:1, IMF, BT, and BW can be simultaneously improved. However, if adopted,
459a reduction in the potential for lean growth is also expected. The extent to which it is
460affordable relies on how much consumers are prepared to pay for high-C18:1 pork
461products.

462

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597

598**Table 1.** Description of the data set used in the analyses

Item	No. of pigs	No. of sires	No. of dams	No. of litters	Mean	SD
Pedigree	93,920	731	18,516	32,315	-	-
Traits						
Body weight at test, kg	85,002	641	16,548	32,211	104.8	12.5
Backfat thickness at test, mm	80,687	642	16,335	31,197	15.6	3.5
Intramuscular fat, %	943	141	543	546	4.9	1.9
Oleic acid, % FA	947	142	544	547	44.8	3.1
Covariates						
Age at test, d	85,194	642	16,601	32,310	180.2	10.7
Age at slaughter, d	2,098	298	1,313	1,370	206.5	14.6
Carcass weight, kg	937	142	542	545	98.4	11.6

599

600**Table 2.** Features of the posterior distribution of the effect of batch, age at slaughter, and
601carcass weight on oleic acid content (C18:1)

Parameter	Mean	SD	Mode	HPD95[2]	k[3]
Batch[1]					
Maximum difference	7.49	0.50	7.54	6.53; 8.49	6.65
Minimum difference	0.21	0.53	0.02	-1.24; 0.83	- 1.12
SD	2.35	0.10	2.34	2.14; 2.55	2.17
Covariates					
Age at slaughter, d	-0.02	0.02	-0.02	-0.05; 0.00	- 0.05
Intramuscular fat, %	0.00	0.14	-0.02	-0.31; 0.26	- 0.25
Carcass weight, kg	0.02	0.01	0.02	0.00; 0.05	0.00

602

603 [1]Maximum difference, minimum difference, and SD among batch effects.

604 [2]HPD95: highest posterior density interval at 95%.

605 [3]k: limit for the interval [k, +∞) having a probability of 95%.

606**Table 3.** Posterior means (SD) of heritabilities (diagonal), genetic correlations (above 607diagonal), residual correlations (under diagonal), additive genetic variance (σ^2_a), litter 608variance (σ^2_c), and residual variance (σ^2_e) for BW, backfat thickness (BT), intramuscular fat 609content (IMF), and oleic acid content (C18:1)

	Trait			
	BW	BT	IMF	C18:1
Trait				
BW	**0.31** (0.01)	0.63 (0.02)	0.27 (0.10)	0.11 (0.11)
BT	0.60 (0.01)	**0.45** (0.01)	0.37 (0.10)	0.22 (0.10)
IMF	0.08 (0.07)	0.15 (0.08)	**0.56** (0.09)	0.47 (0.12)
C18:1	0.20 (0.07)	0.22 (0.08)	0.20 (0.12)	**0.50** (0.08)
Variance				
σ^2_a	29.75 (1.34)	4.11 (0.14)	1.85 (0.36)	2.22 (0.42)
σ^2_c	9.26 (0.37)	0.61 (0.03)	-	-
σ^2_e	57.25 (0.78)	4.45 (0.08)	1.41 (0.27)	2.22 (0.32)

610

611**Table 4.** Features of the posterior distribution of the heritability of oleic acid content 612(C18:1) and the genetic and phenotypic correlations of C18:1 with BW, backfat thickness 613(BT), and intramuscular fat content (IMF)

Parameter	Mean	SD	Mode	HPD95[1]	k[2]
Heritability	0.50	0.08	0.49	0.35; 0.65	0.37
Genetic correlations					
C18:1, BW	0.11	0.11	0.13	-0.10; 0.31	- 0.07
C18:1, BT	0.22	0.10	0.22	0.01; 0.42	0.04
C18:1, IMF	0.47	0.10	0.51	0.24; 0.71	0.27
Phenotypic correlations					
C18:1, BW	0.15	0.02	0.15	0.09; 0.21	0.10
C18:1, BT	0.21	0.03	0.21	0.15; 0.27	0.16
C18:1, IMF	0.35	0.03	0.35	0.28; 0.41	0.29

614

615 [1]HPD95: highest posterior density interval at 95%.

616 [2]k: limit for the interval [k, +∞) having a probability of 95%.

617

618**Table 5.** Posterior means (SD) of heritability of oleic acid content (C18:1) and the genetic
619correlations of C18:1 with BW, backfat thickness (BT), and intramuscular fat content (IMF)
620under alternative models for C18:1

	Covariate[1]				
Parameter	Age	Age + IMF	CW	CW + IMF	ILR[2]
Heritability	0.50 (0.08)	0.51 (0.08)	0.53 (0.09)	0.55 (0.07)	0.49 (0.08)
Genetic correlation					
C18:1, BW	0.11 (0.11)	0.15 (0.11)	0.02 (0.11)	0.02 (0.12)	0.12 (0.12)
C18:1, BT	0.22 (0.10)	0.21 (0.11)	0.16 (0.11)	0.16 (0.12)	0.18 (0.11)
C18:1, IMF	0.47 (0.12)	0.45 (0.14)	0.42 (0.13)	0.46 (0.13)	0.48 (0.13)

621

622[1]C18:1 was adjusted for age at slaughter (Age), age at slaughter plus IMF (Age + IMF),
623carcass weight (CW), or carcass weight plus IMF (CW+IMF).

624[2]The isometric log-ratio (ILR) transformed variables u_1 and u_2 were used instead of IMF
625and C18:1, respectively.

626

627**Table 6.** Indirect response per generation in oleic acid content (C18:1) to restricted
628selection for BW, backfat thickness (BT), or intramuscular fat content (IMF) by
629availability of IMF records

			Expected response			
Recorded traits	Objective[1]	Restriction	BW, kg	BT, mm	IMF, %	C18:1, % FA
BW, BT						
	Max BW	ΔBT = 0	+2.28	0.00	+0.03	-0.03
	Min BT	ΔBW = 0	0.00	-0.93	-0.20	-0.17
BW, BT, IMF						
	Max BW	ΔBT = ΔIMF = 0	+2.26	0.00	0.00	-0.05
	Min BT	ΔBW = ΔIMF = 0	0.00	-0.80	0.00	-0.06
	Max IMF	ΔBW = ΔBT = 0	0.00	0.00	+0.35	+0.17

630

631[1]Trait to maximize (Max) or minimize (Min).

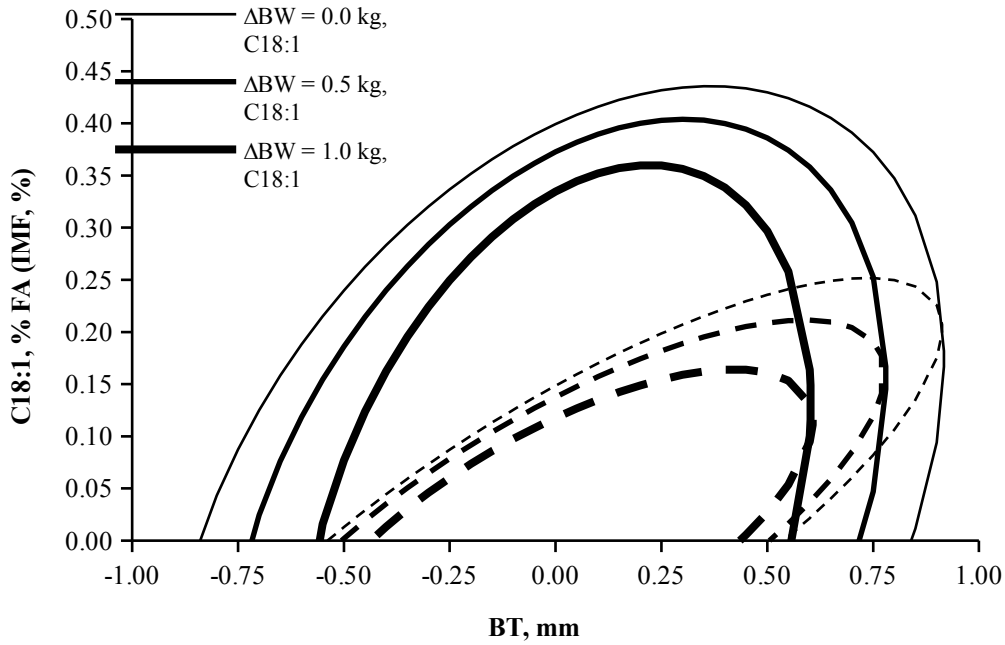
632

633 **Caption for Figure**

634

635**Figure 1.** Maximum expected response for oleic acid (C18:1) (and correlated response
636for intramuscular fat content, IMF) at differing backfat thickness (BT) and fixed BW (0,
6370.5, and 1 kg) responses. Responses are given per generation.

638



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641Figure 1

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